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RESEARCH ARTICLE

Effect of global climate change on the distribution of *Anchomenus dorsalis* (Coleoptera, Carabidae) in Europe

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Abstract

Shifts in a bioclimatic range of *Anchomenus dorsalis* – specialized entomophage – were modeled in the MaxEntsoftware package and are presented on habitat maps. We used two climatic scenarios for the prediction – mild (RCP2.6) and extreme (RCP8.5). Under the considered scenarios, further warming would lead to a shift and extension of the range to the north, northeast, and east and a decrease in the number of populations in the southern regions of Europe. The essential bioclimatic indicators which describe the geographical distribution of *A. dorsalis* are the mean annual air temperature, mean daily amplitude of temperature for each month, the overall amount of precipitation in the coldest quarter of the year, minimum temperature of the coldest month, mean temperature of the warmest quarter of the year, and the annual amount of precipitation. Global warming causes the bioclimatic range of *A. dorsalis* to shift northeast and east in intracontinental territories and west and northwest on islands. Poikilothermic animals may suffer from overheating, and even if they live far in the northern hemisphere, the ability of their organisms to withstand an increase in environmental temperature is limited. Mild winters (with higher temperatures) may increase the mortality of *A. dorsalis* by exhausting their energy reserves. This ground beetle species is an important object in monitoring the condition of natural and agrarian ecosystems, sensitive to the growing global climate changes.

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Keywords
Ground beetles, field entomophages, modeling in Maxent medium, bioclimatic range, bioclimatic factors

Introduction

Entomophages are constant and necessary components of natural and cultivated biocoenoses. Depending on the developed conditions, the decrease in the number of harmful insects occurs under various factors. At the same time, certain groups of entomophages act as leading agents, limiting the pest abundance at different levels (Kryzhanovskij 1983; Puchkov et al. 2020). During the periods with a low number of plant-eating insects, the activity of multifeeding predators acquires significant importance, and in the case of a further increase in the number of phytophages, the leading role is played by specialized species of entomophages (Kotze et al. 2011).

Anchomenus dorsalis (Pontoppidian, 1763) is a species of the carabid tribe Platynini (Kryzhanovskii 1983; Liebherr 1991), distributed throughout Europe from Russia, Norway, Ireland, south to Northern Morocco and Corsica, and east to Turkey, the Caucasus Mountains, and Turkmen SSR (Andersen 1985; Liebherr 1991; Löbl I and Löbl D 2017).

Lindroth (1986) reports that in Denmark, *A. dorsalis* is "very distributed and common. The records from the western and northern parts of Jutland are all from after 1950 and probably represent a recent invasion". Lindroth (1986) also indicates that this species comprises the whole of Europe to 60° N, and Morocco, West Asia, and West Siberia. This author has provided the most detailed ecological characteristic of the species for North Europe: "The least hygrophilous of all *Agonum*, occurring in open meadows and grassland, usually on gravelly or clayey, often limestone soil. Additionally, on arable land, particularly in overwintering crops on heavy soil. It feeds on aphids, insect larvae. Predominantly night-active; during the daytime, it can be found gregariously under stones. The species is most numerous in May–June, which is the breeding season".

In Great Britain (Lindroth 1974), this species is distributed in England, Wales, Scotland, and Ireland, "somewhat local but often abundant; often found in large aggregations under stones in spring". Luff (1992) adds that *A. dorsalis* in Great Britain is “a widespread species in England, Wales, and Ireland is becoming more local and largely eastern in the northern half of Scotland. It is found in dry, open habitat such as grasslands, gardens, and arable land, especially on chalky soils. In cereal fields, it overwinters in field margins (often in large aggregations), and migrates into the fields in the spring, where it is a useful predator on aphids". *A. dorsalis* is winged and breeds in spring (Luff et al. 1989; Luff 1992).

For the territory of the Czech and Slovak Republics, Hurka (1996) reports that the species is macropterous, observed in flight, "very common in unshaded, dry to moderately moist habitats; fields, steppe, pastures, edges of small woods; from

lowlands to mountains, often gregariously". In Spain, the species was found in 20 out of 23 regions (Serrano 2013). It is common in Macedonia, being recorded in 9 of 93 districts (Hristovski and Guéorguiev 2015). The species is common in Bulgaria, where it is present up to 2,000 m in the mountains (Hieke and Wrase 1988; Guéorguiev VB, Guéorguiev BV 1995). This beetle is also common in Greece (Arndt et al. 2011). In Poland, *A. dorsalis* is the most abundant species living in field margins (Sklodowski 2006, 2014; Sklodowski and Garbalinska 2011; Bennewicz and Barczak 2020). In Eastern Slovakia (Baranova et al. 2018), *A. dorsalis* is dominant on agricultural landscape sites.

The species is distributed in Albania (Guéorguiev, 2007), Lithuania (Tamutis et al. 2011), Estonia (Ploomi et al. 2003), Germany (Freude et al. 2004), the Netherlands (Turin et al. 1977), Serbia (Popović and Štrbac 2010) and throughout Ukraine (Kryshtal 1956; Putchkov 2011, 2018; Brygadyrenko 2015a; Putchkov et al. 2020) and Moldova (Karpova and Matalin 1993; Nekuliseanu and Matalin 2000). Kryzhanovskij et al. (1995) provided a detailed characteristic of species in the territory of the former Soviet Union: the Urals, the middle stretch of West Siberia, South of West Siberia, the plains of Kazakhstan, the plains of Central Asia, and a part of Transcaucasia, Tian-Shan, mountains of South-East part of Central Asia, the Altais-Sayan Mountains, Transbaikalia, Cisamuria and the Maritime Provinces. The beetle is also a dominant species in the Chakilkalyan Mountains (Uzbekistan) (Khalimov 2020).

Zamotajlov and Nikitsky (2010) report that in the territory of the Republic of Adygea, this species of ground beetle is "very common: polytopic mesophile, inhabits several zonal communities. Occurs in agrocoenoses". Moderately xerophilic biotopes, including agricultural soils, clay, and even chalky soils (Liebherr 1991). Similar to other species of ground beetles, this beetle is characteristic of zonal shifts in habitats: it inhabits more mesophilic habitats in the south of its range and becomes more xerophilic in the north (Sigida 1993; Brygadyrenko 2015c, 2016).

Anchomenus dorsalis is a zoophage, surface-litter stratobiont (Sharova 1981). It is known as a specialized predator of wheat aphid (*Schizaphis graminum* Rondani, 1852), wheat bulb fly (*Delia coarctata* (Fallen, 1825), frit fly (*Oscinella frit* (Linnaeus, 1758), cabbage moth (*Mamestra brassica* (Linnaeus, 1758), bird cherry-oat aphid (*Rhopalosiphum padi* (Linnaeus, 1758), pea aphid (*Acyrthosiphon pisum* Harris, 1776), common pollen beetle (*Brassicogethes aeneus* (Fabricius, 1775)). This species is the most important regulator of the number of agricultural pests and can live in polluted and anthropogenically transformed territories (Hurka and Jedlickova 1990; Kosewska et al. 2013; Halinouski and Krytskaya 2014; Brygadyrenko 2015b). This species is especially abundant in the territory of certain urban agglomerations (Magura et al. 2008; Kirichenko and Danylkiv 2011; Bednarska et al. 2017; Faly and Brygadyrenko 2018; Kirichenko-Babko et al. 2019). Many authors note *A. dorsalis* as a typical inhabitant of fields in Belarus (Aleksandrowicz 2014), Krasnodar Krai, and the Republic of Adygea (Zamotajlov and Nikitsky 2010). In south Slovakia, it

was an abundant species on arable land (Langraf 2016) and was dominant in wheat fields in Serbia (Popović and Štrbac 2010).

The objective of this research was to characterize the ecological niche and areal changes of critical agricultural entomophages – *A. dorsalis*.

Material and methods

The materials for this study were the field collections made by the authors of the article, and the data obtained from the publications and the open database GBIF – 503 points (*Anchomenus dorsalis* (Pontoppidan, 1763). In: GBIF.org (12 January 2021) GBIF Occurrence Download: https://doi.org/10.15468/dl.9g2ev6). For the bioclimatic modeling (Avtaeva et al. 2019, 2020), we used the data of the Global DataBase WorldClim (www.worldclim.org): 19 bioclimatic variables with 2.5 min spatial resolution. The field collections (100 points) were carried out in different years in Dnipropetrovsk, Zaporizhia, Kharkiv, Mykolaiv, and Donetsk Oblasts of Ukraine. In the Czech Republic, the material was collected from eight plots in foothill and highland districts. Over 3,000 specimens of *A. dorsalis* were collected. To capture the beetles, we used soil traps and caught the insects manually under the plant remains and stones. As for the traps, we used plastic cups of 0.5 L capacity with 4% formalin or vinegar. At each site, 20 traps at 10 m distance, one from the other, were installed. The beetles were extracted once in ten days.

In our study, we used RStudio software to reduce the correlation between the climatic characteristics by detecting and deleting highly correlated variables. Using additional capacities provided by some software, including RStudio, SDMtoolbox, ENMTools, we improved the quality of the model, particularly the data on the presence and climatic characteristics. The analysis dealt with six variables, the correlation between which did not exceed 0.75: average annual air temperature; average daily temperature amplitude for each month; overall amount of precipitation in the coldest quarter of the year; the lowest temperature of the coldest month, mean temperature of the warmest quarter of the year; the overall annual amount of precipitation.

Using the same software, we filtered the points of occurrence of the species to obtain a more even distribution of them. Thus, the analysis involved 355 points. To avoid a selection shift toward territories with the highest number of points, we created a bias file (see Suppl. material 1: Map 1).

To increase the predicting ability of the model and balance its correspondence and predictive ability, we created a csv file "enmeval-results" in the same software. Modeling was made according to the settings corresponding to the lowest values of AICc and $\Delta AIC = 0$.

In all modeling cases, we used the climatic model CCSM 4 (Community Climate System Model). We took into account two scenarios of climate change: RCP2.6

(suggests an increase in global temperature on average by 0.9 °C) and RCP8.5 (increase by 4.1 °C) (Jia et al. 2019).

For the work with the layers, we used QGIS 3.18.1 software (Quantum GIS, 2020). The potential range was modeled using Maxent 3.4.4 software (Phillips SJ, Dudík M, Schapire RE, 2017: Maxent software for modeling species niches and distributions (Version 3.4.4), http://biodiversityinformatics.amnh.org/open_source/maxent). Multidimensional analysis of the climatic niche applied the maximum entropy method; the factors that make the most significant impact on the current distribution of *A. dorsalis* were distinguished.

To verify the model, we developed the area (AUC) under the ROC curve (ROC – receiver operating characteristic, AUC – area under the curve) was used. To evaluate the developed model, we set 25 random test percentages, i.e., out of all points of occurrence, the software randomly selects 25% for the following test of the output model. We set a threshold of 10 percentiles, which implied excluding 10% of the points in the species' threshold climatic conditions out of the process.

AUC measures the ability of the model to distinguish places where a species is present and places where it is absent and varies from 0 to 1. In our model, AUC equaled 0.985 ± 0.002, which means the likelihood of a species being present in the given area is 98.5%, i.e., the reliability of the developed model is relatively high (Fig. 1).

The goal of modeling as a task of binary classification implies adding points of absence to the developed selection. In this study, the random selection includes 75,000 (max number of background points), which, according to El-Gabbas and Dormann (2018), may contribute to the representativeness of the analysis. Because the points of presence amounted to over 500, we used different functions of the feature predictors (El-Gabbas and Dormann 2018).

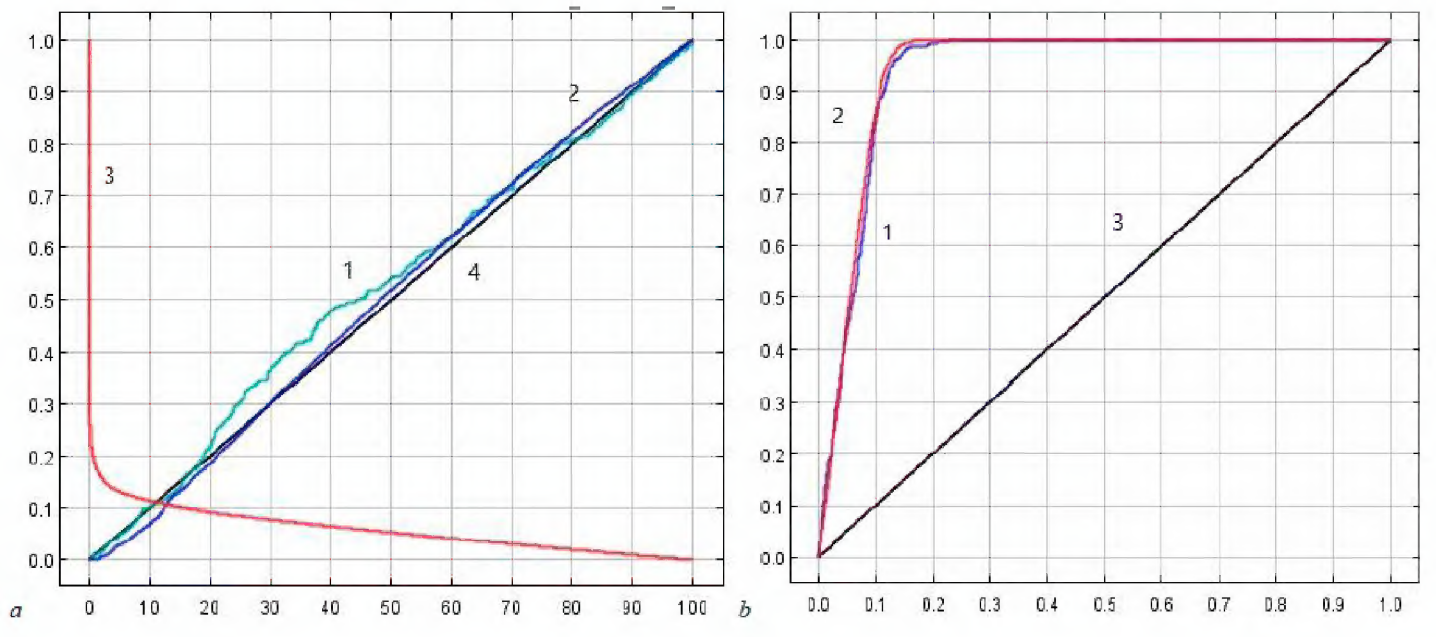

Figure 1. Analysis of the accuracy of the model of possible distribution: **a** – omission and predicted area for *A. dorsalis* (**1** – test data, **2** – training data, **3** – a fraction of initial data which were predicted, **4** – predicted emissions); **b** – trend of the operative curve AUC (**1** – test data, **2** – training data, **3** – random prediction).

An essential stage of the modeling is the selection of traits, as they determine the adequacy of the model. For this purpose, we used bioclimatic parameters from the WorldClim database, which were filtrated according to the significance of the species' spatial distribution. The remaining variables were then processed through the algorithm of sequential exclusion of traits while continuously monitoring the AUC parameters.

In the MaxEnt program, the range of conformity varies from 0 to 1. We estimated the areas of both current and predicted bioclimatic distribution ranges of the studied species.

Analysis of the points of occurrence and bioclimatic parameters in the MaxEnt medium allowed us to determine the most significant ecological factors for the distribution of this species.

To study the possible changes in the spatial distribution of this species in the face of climate change, we considered the European part of the range.

Results

Using MaxEnt software, we developed a table of assessment of the significance of bioclimatic parameters that affect the distribution of *A. dorsalis* (Table 1).

Analysis of the testing results revealed that the most significant factor was Bio 2 – mean daily amplitude in temperature for each month after the permutation test. The second by significance was Bio 1 – mean annual air temperature; a significant factor was Bio 10 – mean temperature of the warmest year quarter and Bio 19 – the overall amount of precipitation in the coldest year quarter. Bio 12 – overall annual precipitation took the lowest effect on the modeling results in conditions of permutation.

Table 1. Contribution of bioclimatic parameters to the distribution of *Anchomenus dorsalis*

Bioclimatic parameters	**Percent contribution**	**Significance of permutation**
Mean annual air temperature	29.2	22.2
Mean daily temperature amplitude per month	19.9	26.1
The total amount of precipitation in the coldest quarter of the year	18.0	15.3
Minimum temperature of the coldest month of the year	15.8	11.6
Mean temperature of the warmest quarter of the year	11.4	20.7
The overall annual amount of precipitation	5.7	4.2

The potential range of *A. dorsalis* almost coincides with its actual range. The logarithmic 10-percentile threshold obtained for this species equaled 0.2. The scale of appropriateness or comfortness of the habitat consists of 4 gradients: 0.8–0.9 – the most appropriate territories (red color); 0.6–0.8 – appropriate territories (orange); 0.4–0.6 – less appropriate (yellow), 0.2–0.4 – the least appropriate territories (green); < 0.2 – territories inappropriate for the species. To estimate the areas, we used two categories: 0.6–0.9 – favorable territories; 0.2–0.6 – less favorable territories.

Graphical analysis of species distribution on particular factors allowed us to distinguish the optima for each one of them. The optimum average annual air temperature ranges within +5…+12 °C (Fig. 2a). The range of the mean daily amplitude of the temperature for each month changes within the range of 5–10 °C (Fig. 2b). The most favorable overall amounts of precipitation of the coldest quarter of the year are within 100–300 mm (Fig. 2c). The minimum temperature range of the coldest month for *A. dorsalis* equals –10…+2 °C (Fig. 2d). The mean temperature of the warmest quarter of the year is +15…+25 °C (Fig. 2e). The annual overall amount of precipitation for this species amounts to 500–1,100 mm (Fig. 2f). Thus, the optimum of the parameters most important to *A. dorsalis* is relatively narrow.

Using QGIS software, we visualized the current bioclimatic range of *A. dorsalis* and the expected distribution ranges under two global climate change scenarios for 2050 and 2070 (Figs 3–7). Bioclimatic parameters indicated as 2050 included 2041 – 2060 and 2070 – 2061 – 2080.

According to the model of the current bioclimatic range of *A. dorsalis*, which we obtained, the optimum conditions develop in the south of Sweden, Norway, Denmark, Germany, the Netherlands, Belgium, north-east and south-east parts of France, the northwest part of Switzerland, north part of Spain, south-east Great Britain. Such territories include Italy, Serbia, Slovenia, the Czech Republic, west and east Hungary, south Romania, Bulgaria, northwest Poland, the central part of Moldova, south-west and east Ukraine, western parts of Belarus, Lithuania, Latvia, Estonia, the north coast of Turkey, south Russia, Stavropol Krai and Krasnodar Krai, Georgia, west coast of the Caspian Sea, including parts of Dagestan and Azerbaijan, Armenia. In the south direction, the level of favorability decreases, equaling 0.6–0.8. In the northeast direction, the distribution of the species we study becomes less continuous; northeast intracontinental territories become less suitable.

The area of the current bioclimatic range of *A. dorsalis* in the study territory accounts for 3,990,418 km^2. The model produced for scenario 2.6 predicts that the area will be 4,736,477 km^2 in 2050. By 2070, the area of the range will continue to increase, accounting for 4,806,320 km^2 (Table 2). By 2050, according to scenario RCP2.6, the area of optimum territory will increase 1.5-fold (0.6–0.9), and by 2070, an insignificant increase will occur.

Thus, the distribution range broadens northeast and east inside the continent and expands west and northwest on the islands during 2041-2060. This is observed

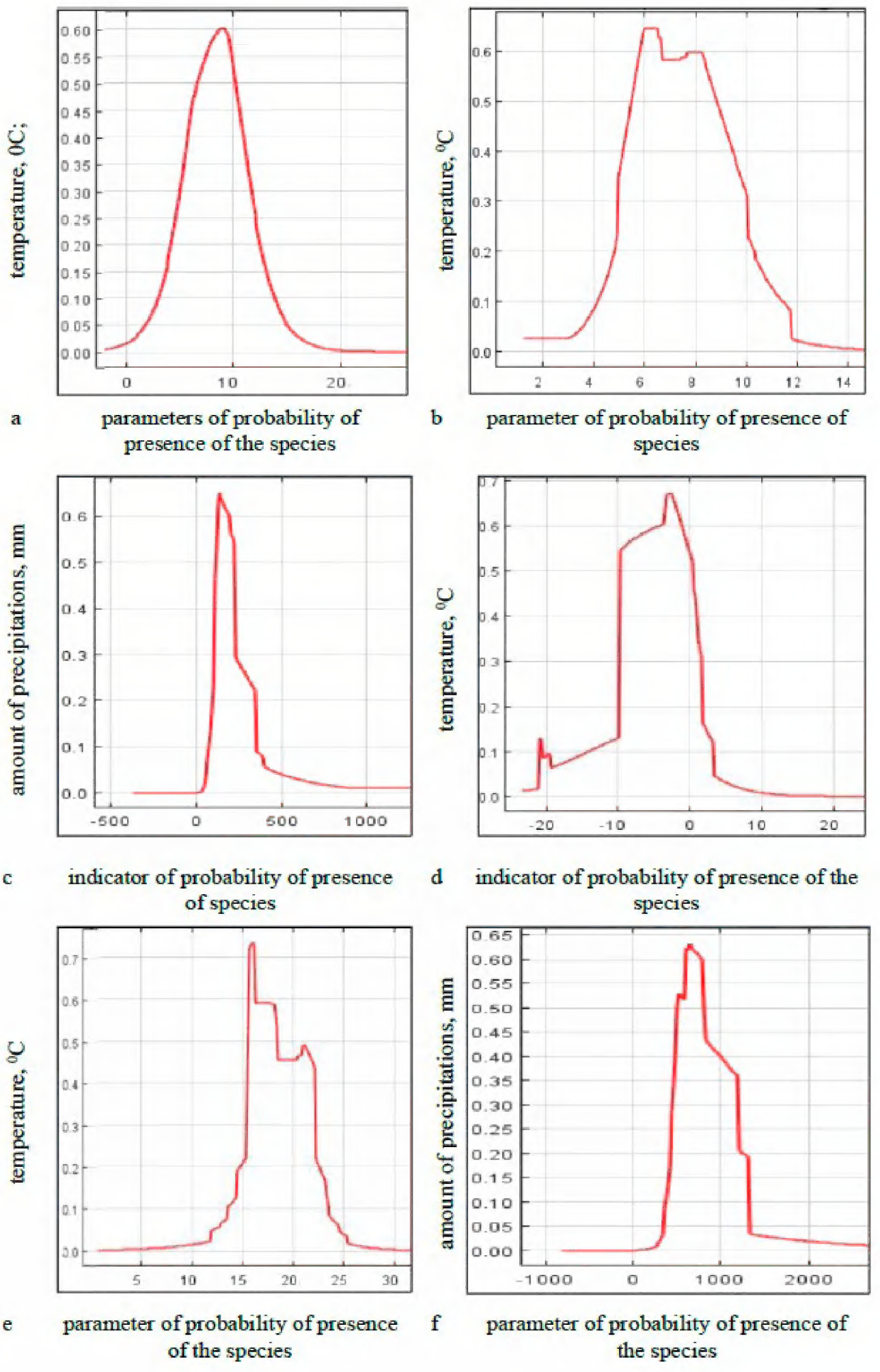

Figure 2. Range of values of bioclimatic factors most important for *Anchomenus dorsalis*: **a** – graph of mean annual air temperature; **b** – graph of mean daily temperature amplitude for each month; **c** – graph of precipitation overall amount in the coldest quarter; **d** – graph of minimum temperature in the coldest month; **e** – graph of mean temperature in the warmest quarter; **f** – graph of precipitations overall annual amount.

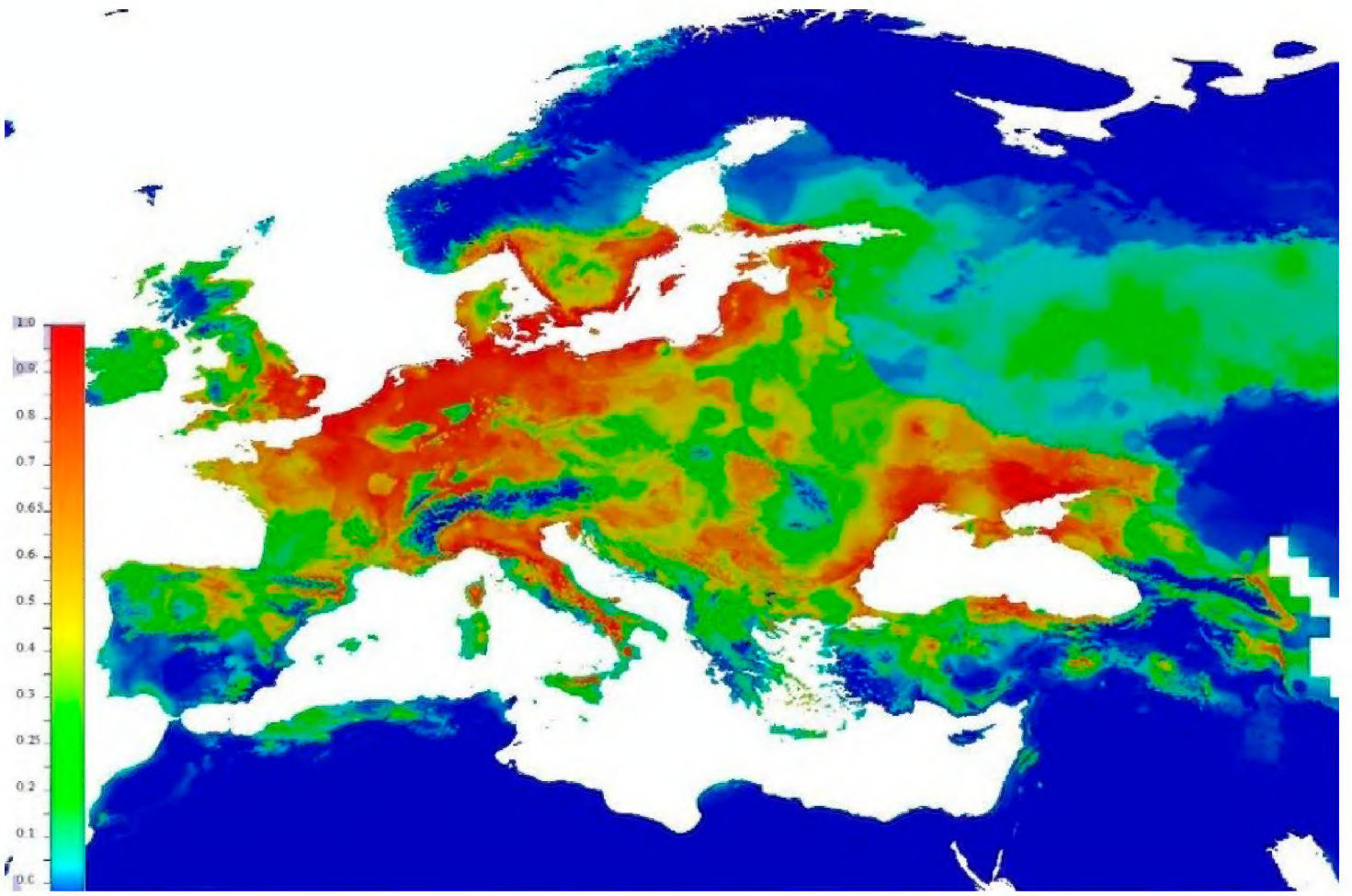

Figure 3. Current bioclimatic range of *Anchomenus dorsalis*: in red – the most favorable zones for habitation (comfort index – 0.8–0.9), in orange – close to optimal (comfort index – 0.6–0.8), in yellow – less suitable (comfort index – 0.4–0.6), in light-green – unsuitable (comfort index – 0.2–0.4).

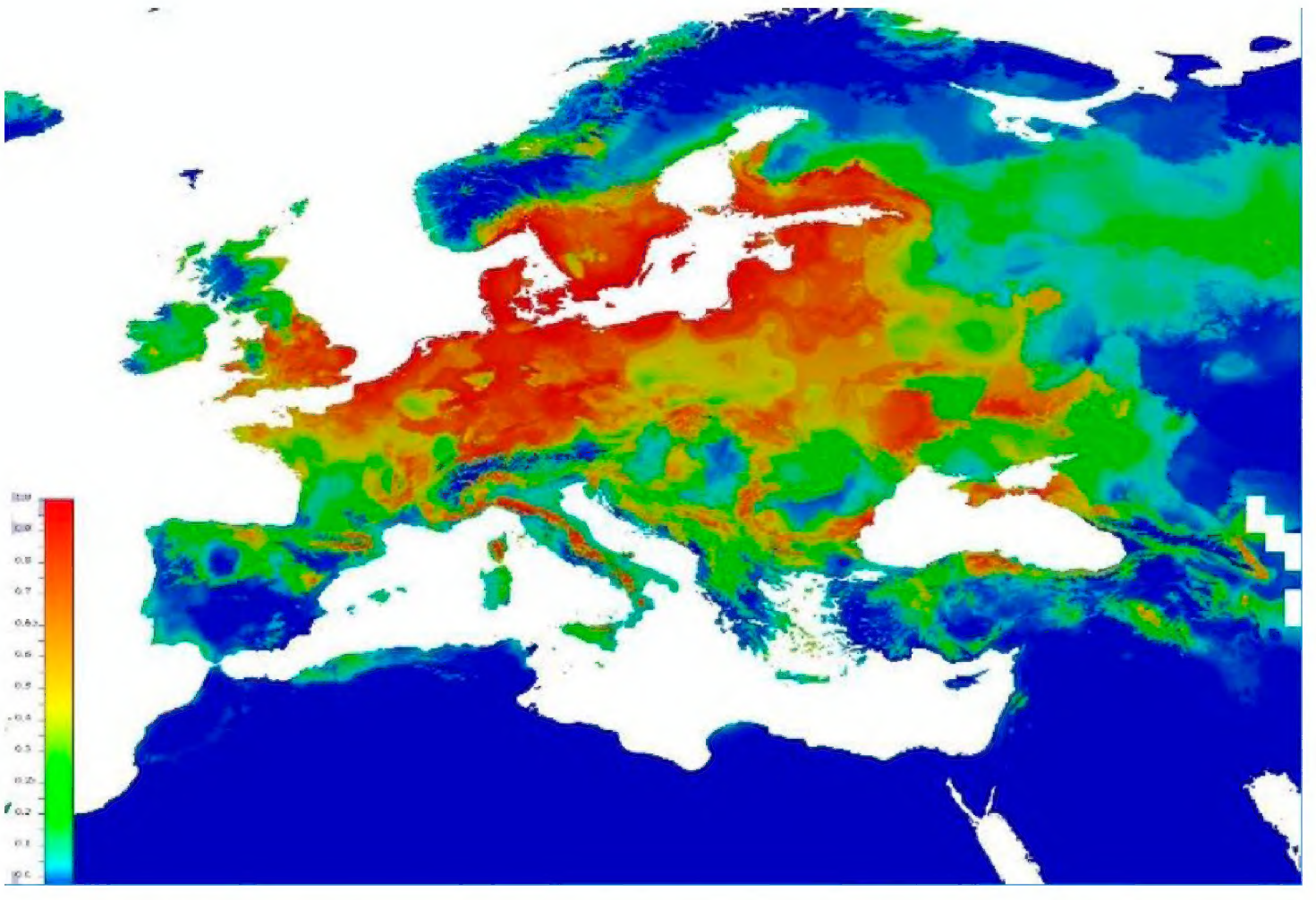

Figure 4. Bioclimatic range of *Anchomenus dorsalis* as of 2050 according to scenario RCP2.6: description of color gradation – see Fig. 4.

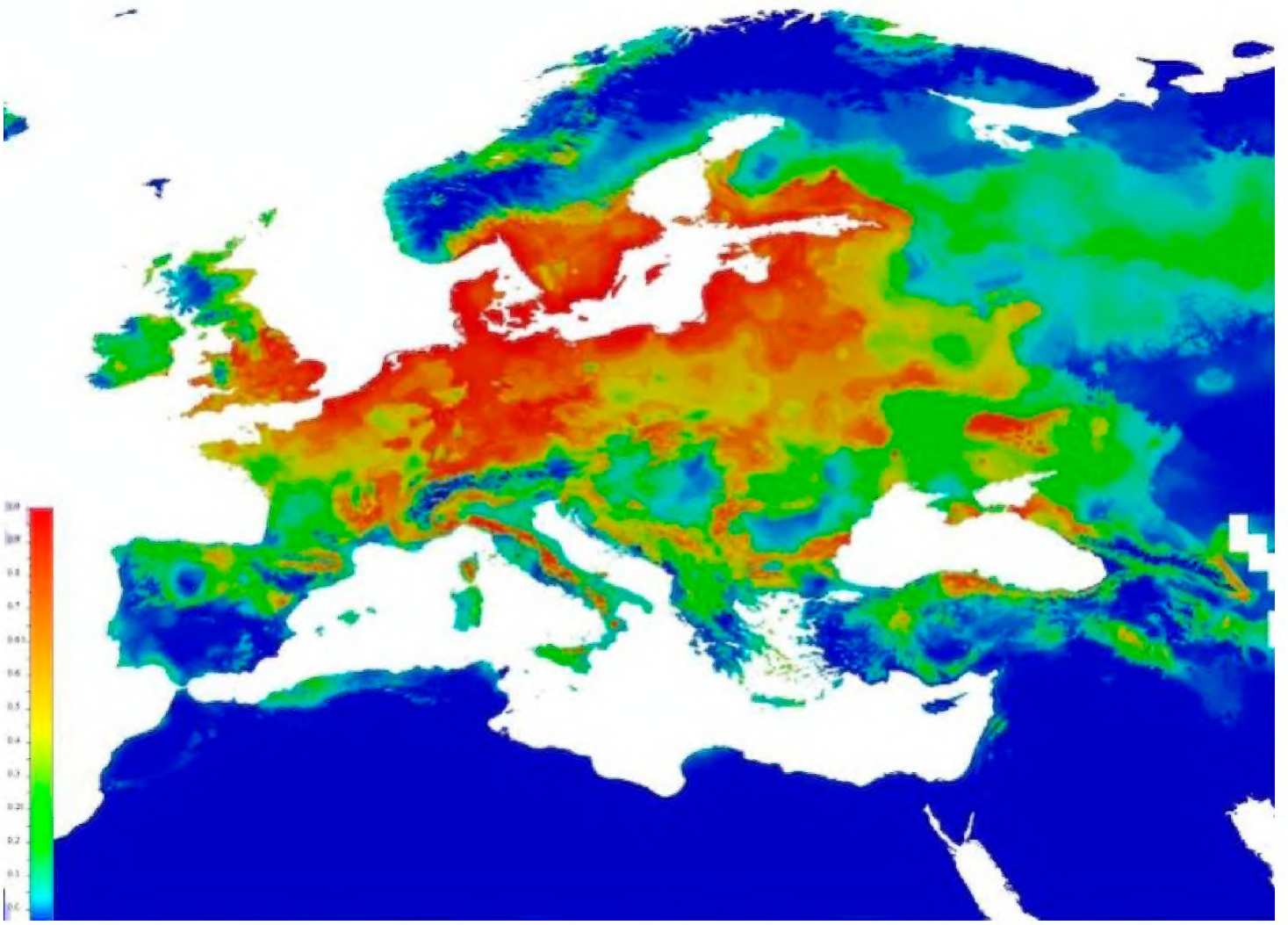

Figure 5. Bioclimatic range of *Anchomenus dorsalis* as of 2070 under scenario RCP2.6: description of color gradation – see Fig. 4.

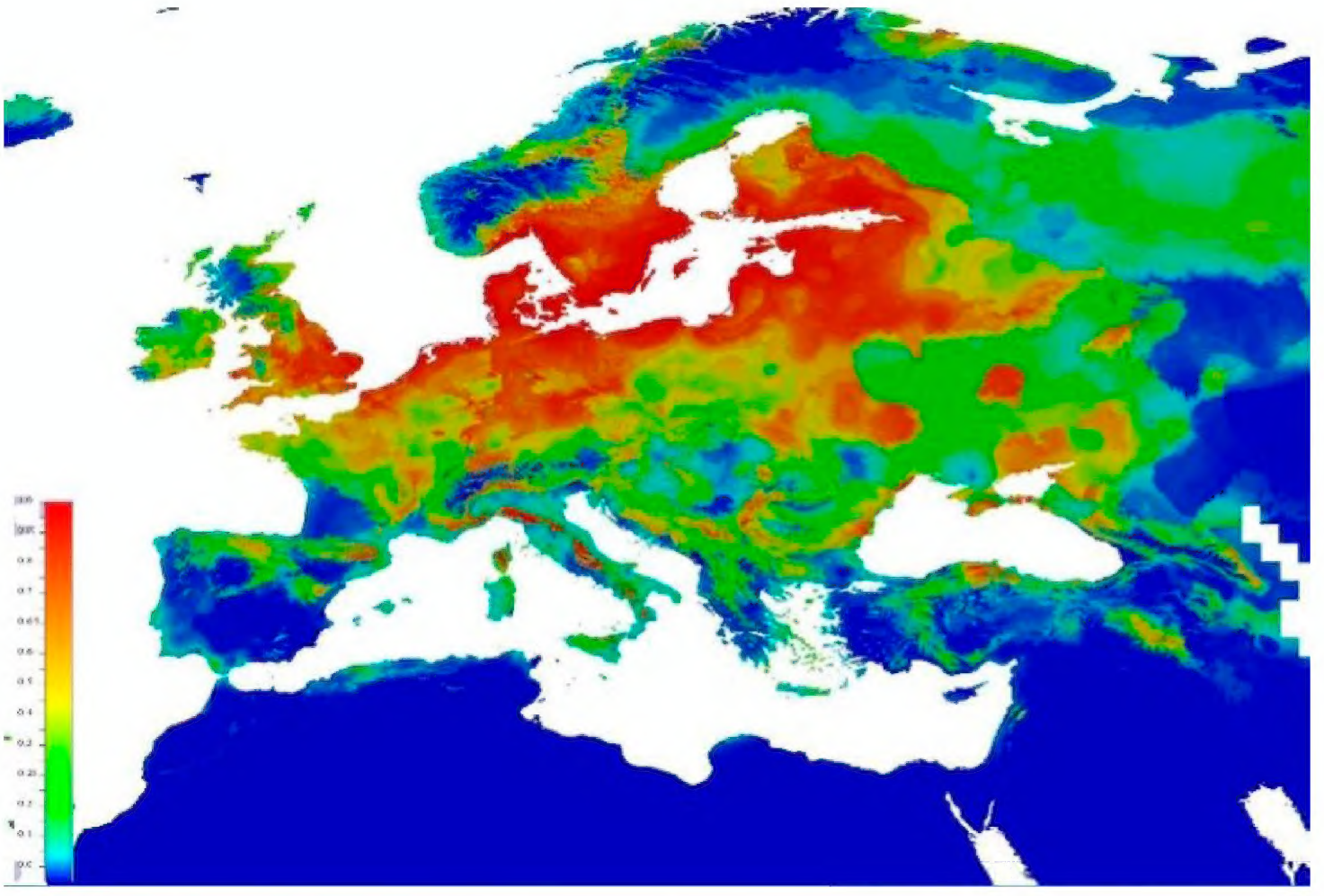

Figure 6. Bioclimatic range of *Anchomenus dorsalis* as of 2050 under RCP8.5: description of color gradation – see Fig. 4.

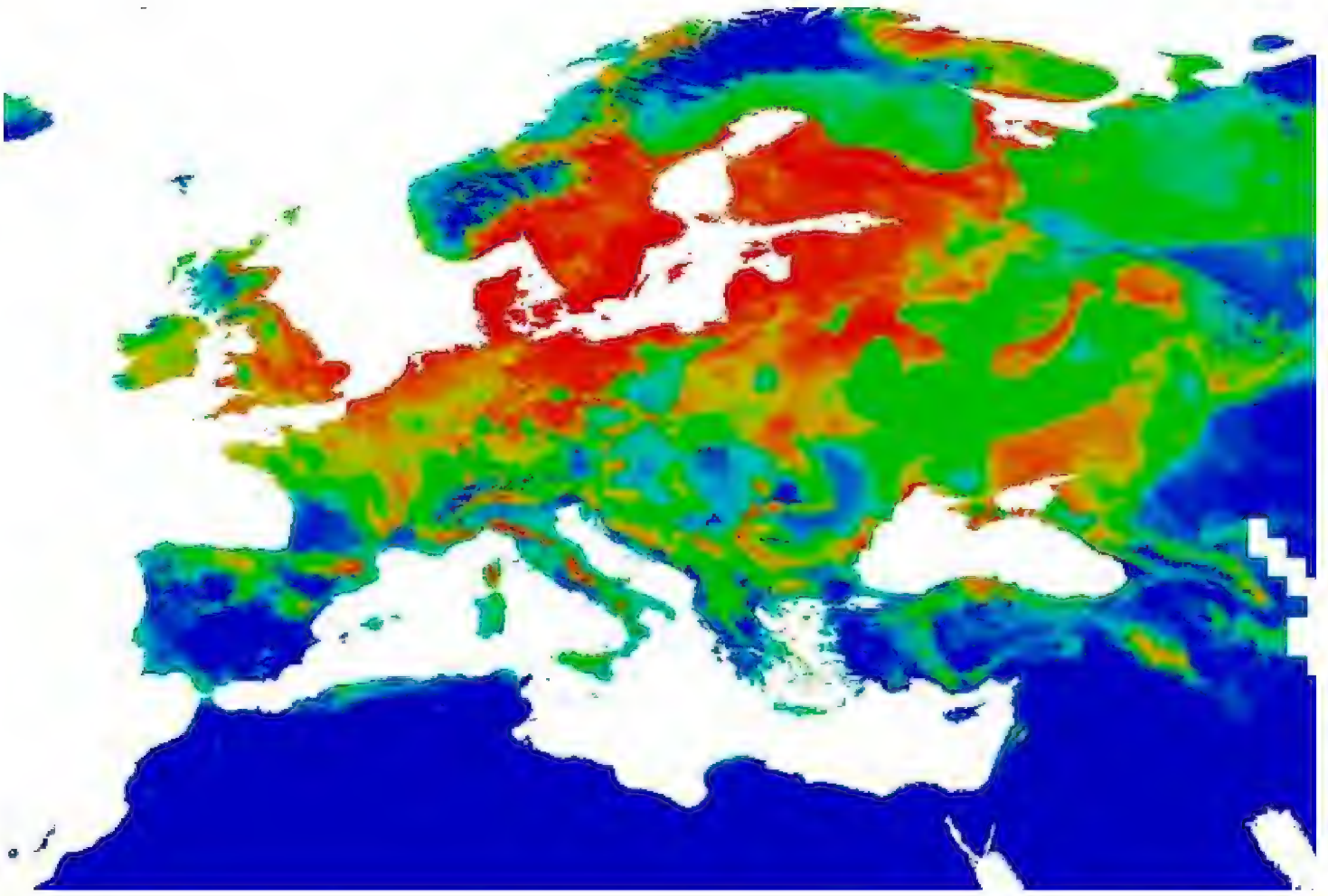

Figure 7. Bioclimatic range of *Anchomenus dorsalis* as of 2070 under scenario RCP8.5: description of color gradation – see Fig. 4.

in Great Britain and Ireland. In Spain, the borders shift to the north. With the increase in mean annual temperature, the borders of the most comfortable territories broaden to the north of Denmark and Sweden. In the east, more favorable conditions develop along the coast of the Gulf of Finland, northwest territories of Belarus, Kursk, Voronezh, Moscow Oblasts. The eastern border reaches the Krasnoiarsk Krai. In the time interval of 2061-2080, the range continues to expand east.

Under the extreme scenario RCP8.5, the time interval between 2041-2060 is characterized by some decrease in the climatic range along the southern borders of Eastern Europe, and its shift east can be seen. By 2060, a significant decrease in the climatic range of *A. dorsalis* may occur in Transcaucasia.

Table 2. Size of bioclimatic range (km^2) of *Anchomenus dorsalis* under scenario RCP2.6

Period	**Parameter of bioclimatic suitability of habitat**		**Total area**
	0.2–0.6	**0.6–0.9**	
Currently	3 050 669	939 748	3 990 418
RCP2.6, 2050	3 286 708	1 449 769	4 736 477
RCP2.6, 2070	3 254 829	1 551 491	4 806 320

At the same time, the overall area of the range under scenario RCP8.5 increases due to its expansion northeast. By 2050 and 2070, the territories with the suitability of 0.6–0.9 will have increased (Table 3).

Table 3. Size of bioclimatic range (km^2) of *Anchomenus dorsalis* under scenario RCP8.5

Period	**Parameter of bioclimatic suitability of habitat**		**Total area**
	0.2–0.6	**0.6–0.9**	
Currently	3 050 669	939 748	3 990 418
RCP8.5, 2050	3 640 100	1 623 635	5 263 735
RCP8.5, 2070	3 817 860	2 105 507	5 923 367

Discussion

The developed model of the bioclimatic range of *A. dorsalis* shows that, while the beetle advances south from the north, the current range comprises a zone of mixed broad-leaved forests, forest-steppe and steppe, the Mediterranean zone, and a zone of altitudinal zonation. Its distribution is affected by four temperature factors (daily amplitude of the temperature course, temperature of the warmest year quarter, the lowest temperature of the coldest year quarter, and mean annual temperature) and two factors related to moisture (overall precipitation in the coldest year quarter and overall annual precipitation, the latter to a less extent). According to the predicted models, global warming leads to the shift of the bioclimatic range of *A. dorsalis* northeast and east. In the islands, it would shift west and northwest. This is coherent with the Intergovernmental Panel on Climate Change (IPCC) data, which predicts a 1.4–5.8 °C increase in the mean global temperature from 1990 to 2100 (Jia et al. 2019). The most significant increase in mean annual temperature is expected in South Europe (Spain, Italy, Greece), North Europe (Finland, and west Russian Federation), while the least increase would occur along the Atlantic coast. Almost all lands shall face a higher number of hot days; the number of cases of extreme precipitation is expected to grow, while the days with a small amount of precipitation would decrease for many regions in extratropical latitudes of the Northern hemisphere, and the number of cold days will decrease almost everywhere around the globe.

For most terrestrial regions, prognoses indicate a decrease in the amplitude of the daily temperature course and a decrease in snow accumulation and its earlier melting. Both factors are important for our species. For the life cycle and seasonal dynamics of *A. dorsalis*, the parameters of winter temperature are significant. Our modeling results indicate that the distribution of *A. dorsalis* depends on the temperature of the coldest month of the year. This fact was confirmed by Knapp and Uhnavá (2014), who determined that the survivability of males and females is af-

fected by winter weather conditions. In low temperatures, the survivability of the beetles is poor (13.0% overall).

This correlates with the predictions of climate change for the XXI century, stating that temperature fluctuations will increase overwintering according to the global tendency. In South Europe in summer, it becomes twice faster compared with North Europe. Presumably, cold winters will completely disappear in this century, and hot summers will occur increasingly often. The most significant increase in near-surface temperature is expected in winter, even greater in the north, while the minimum would be seen in summer (Batschynskaja et al. 2020; Koshelev et al. 2020; Avtaeva et al. 2021; Makaida et al. 2021). The results of the study indicate that poikilothermal animals can suffer overheating, and even if they live far in the northern hemisphere, their ability to protect their organisms against the increase in the environmental temperature is limited. There are reports that mild winters (with higher temperatures) cause mortality by depleting energy reserves, whereas harsh winters (with low temperatures) cause death from cold trauma.

A. dorsalis has a variable life cycle (Basedov 1994; Matalin 2007) in the territory of Russia. *A. dorsalis* is a winter-spring species with a broad range of reproduction period, the development of which in males and females occurs in conditions of prolonged daylight, while the short days slow their warming (Matalin 2007). Winter-spring species breed in the early vegetative period: from mid-late March to mid-late May. Some of them in favorable conditions begin to ovideposit already in late winter, completing the breeding by mid-spring (Matalin 2007).

Analysis of the contribution of the factors revealed the importance of mean daily temperature amplitude for this species, as confirmed by the studies (Matalin, 1998, 2003). In our opinion, this may be related to the fact that in the XXI century, the difference between the lowest and highest daily temperatures in 2070 will decrease practically throughout the analyzed territory. By the mid-XXI century, an almost ubiquitous decrease in the number of frosty days in the year is expected (i.e., days with minimum daily temperature below 0 °C), equaling 20–30 days. By the late XXI century, these changes, on average, will increase two-fold. An increase is seen in the duration of periods with the maximum daily temperature that exceeds 25 °C: much more significant in the northern and highland regions.

Both scenarios indicate some increase in the area, with shifts to the north and changes in the parameter of appropriateness in the intracontinental territories.

The shift of the habitat range of this species upsets the trophic relations and competitive interactions with other species of field ground beetles. Volatile compounds produced by disturbed adults *A. dorsalis* were surveyed by Bonacci et al. (2011a, 2011b). Imagoes had a considerably greater content of four major volatile compounds (undecane, heneicosane, Z-9 tricosene, and tricosane), of which undecane was released in much more considerable amounts by disturbed adults compared to undisturbed beetles.

Makarov and Bokhovko (2006) indicate that "larvae of Brachinus elegans were most often found on pupas of Amara, although some individuals developed on pu-

pas of *Anchomenus dorsalis* (Pontoppidan, 1763). Perhaps, this species is also a food object of larvae of Brachinus, as indirectly indicated by the coincidence of periods and their season activity".

Bonacci et al. (2008) noted the similarity in odor and color between *Brachinus sclopeta* and *A. dorsalis*: *B. sclopeta* may benefit from reducing individual predation risk due to an increased number of aggregated prey (dilution effect), while *A. dorsalis* may increase the benefit both from the dilution effect and from the greater chemical defense of *B. sclopeta*. Zetto Brandmayr et al. (2006) found essential differences in the occurrence of rubbing behavior towards aposematic and non-aposematic species, as *A. dorsalis* displayed the rubbing only towards the former (*Brachinus sclopeta*). The paper presentation tests demonstrated that the odor of *B. sclopeta* was sufficient to provoke rubbing in *A. dorsalis*.

In color, *A. dorsalis* resembles beetles of *Brachinus* genus, and it is often found in their aggregations (Bonacci et al. 2011a). By having an appearance similar to *Brachinus* beetles that produce benzoquitones, *A. dorsalis* is much more rarely attacked by natural predators such as *Crocidura leucodon* (Insectivora, Soricidae), *Ocypus olens* (Coleoptera, Staphylinidae) and *Podarcis sicula* (Reptilia, Lacertidae), which tend to prefer non-aposematic prey (Bonacci et al. 2008b). When catching *B. sclopeta* or *A. dorsalis*, lizards *Podarcis sicula* always tossed their head and rubbed the snouts on the soil (Bonacci et al. 2008a), while no such behavior was seen during preying on other ground beetles, which were easily caught and consumed.

As for diet contribution, beetles *A. dorsalis* were observed incorporating more plant-based resources in organically managed cereal fields than in the flowering fields (Mader et al. 2018). The study (Pajač Živković et al. 2018) showed the positive effect of exclusion nets on *A. dorsalis* in an apple orchard of Croatia, thus confirming their value in assessing the introduction of new agricultural measures into practice. Marrec et al. (2017) evaluated the impact made on activity and density of *A. dorsalis* by local crops, current year, landscape composition, and their interaction, and inter-annual changes in landscape composition due to crop rotations. Pitfall traps were installed in 188 fields in France, and the results revealed the beetle to be more abundant in oilseed rape and landscapes with a higher proportion of oilseed rape in the previous year.

After overwintering, *A. dorsalis* needs to replenish its fat stores to prepare for migration and subsequent reproduction. Therefore, Toft and Nielsen (2017) suggest that these primarily carnivorous beetles may consume overwintered fruits. The beetles were observed to have increased heat emission while feeding on foods rich in sugar and protein against food rich in lipids (Toft and Nielsen 2017). They were co-existing predatory species of Carabidae that manifest notable segregation of the macronutritional niches (fat/protein ratio) (Toft et al. 2019).

In the face of global warming, the trophic activity of many species of ground beetles in agrocoenoses increases, thus limiting the number of pests in fields. According to Frank and Bramböck (2016), global warming will cause this species to consume more pest beetles. In their laboratory experiments, *A. dorsalis* consumed

much more food in the containers, where the temperature was 3 °C and 5 °C higher than in the control containers (Frank and Bramböck 2016).

Experiments on limiting protein or fat components of the diet of this species of ground beetle revealed that the imagoes need both fat and protein in their diet simultaneously (Jensen et al. 2012). When the beetles were restricted to two imbalanced diets, they balanced between overeating and undereating lipids and proteins by consuming such a composition that maximized egg production in those conditions.

This species of ground beetle is resistant to persistent hunger, the probability of which also increases in the condition of global climate change. In a laboratory experiment, *A. dorsalis* imagoes were outstandingly resistant to starvation: having no food, males survived up to 137 days and females up to 218 days at a temperature of 20 °C (Knapp 2016). Throughout overwintering, *A. dorsalis* changed the mean structural body size, likely due to size-specific winter mortality. The effects of overwintering varied between years, perhaps depending on the specific weather conditions of a particular winter (Knapp 2016).

In the morphological structure of populations of *A. dorsalis*, similarly to other species of ground beetle (Baranovska and Knapp 2014; Komlyk and Brygadyrenko 2019, 2020), subtle changes were found that affect the vitality of separate individuals and populations in general. Knapp and Uhnavá (2014) examined the effects of female structural body size (manifested in the length of the elytra and the width of the pronotum). The results revealed that the structural body size of females and the feeding of adults positively influenced egg production. Moreover, feeding had a significant effect on total fecundity (the number of eggs laid plus the number of mature eggs in ovaries), whereas structural body size, feeding before winter, or behavior had no significant effect on the winter survival of *A. dorsalis* females (Knapp and Uhnavá 2014).

Beetle body weight was corrected for its structural body size, representing an animal's energetic reserve and indicating the organism's health. The body condition was severely affected by overwintering (the post-overwintering individuals collected in spring were in worse condition than pre-overwintering individuals collected in autumn), especially in the case of males (females were in better condition than males) (Baranovska et al. 2014).

In shifting their range, the beetles will be facing new types of soil, technologies of its treatment and fertilization, and will be obliged to inhabit new agrocoenoses, not similar to the ones they have inhabited before. In the wheat fields of North-East Poland, the species dominates, although according to Kosewska et al. (2014), the abundance of the species on six wheat fields, each cultivated using either conventional or non-inversion soil tillage, was studied. In the three fields where the non-inversion method of cultivating wheat was employed, 178-208 specimens of *A. dorsalis* were caught in each, and in the fields treated using the conventional method – only 55–70 specimens.

A. dorsalis is common in the fields of winter oilseed rape (*Brassica napus* L.) (Zaller et al. 2008). However, a field experiment on increasing the predator number did not lead to a decrease in the number of rape pests: after 25 imago/m2 of *A. dorsalis* had been introduced to the enclosures without predators, the stem weevils emerged in similar numbers to those in the enclosures to which the predators had free access. *A. dorsalis* is one of the 10 most abundant ground beetles among the 42 species living in the rape fields in the European Union (Williams et al. 2010). Out of the 11 studied rape fields, the species was found in 7 of them in Germany, Sweden, Great Britain, Estonia. The species is common in barley fields in Slovakia, although its abundance does not exceed 10% of the total ground beetles (Porhajašová et al. 2008). Spatially, the *A. dorsalis* beetles were coherent with *Ceutorhynchus* spp. larvae during two peaks in the abundance of *Meligethes aeneus* (F.) and Collembola in June (Warner et al. 2008). Both spatially and temporally, *A. dorsalis* correlated with larvae of *Ceutorhynchus pallidactylus* (Marsham), the cabbage stem weevil, and *Ceutorhynchus assimilis* (Paykull), the cabbage seed weevil when they are most vulnerable to epigeal predators. Thus, *A. dorsalis* is a great candidate for conservation biocontrol (Warner et al. 2008). *A. dorsalis* dominated in sixteen 1–4-year-old wildflower areas (Frank et al. 2007). The species is the third most abundant ground beetle of the 91 species of this family, caught in the fields of the Czech Republic (Veselý and Šarapatka 2008).

Conclusion

Detection of development patterns for various species distribution ranges, including entomophages, is a fundamental issue. It is possible to assess the perspectives of species further existence and their range patterns under the influence of different factors. With the emergence of new methods and technologies, modeling the range of species based on their relations to the climatic parameters, geosystem characteristics, and the structure of the main habitats has become possible. Modeling the geographic distribution of biological species using a new method of maximum entropy based on the Maxent software allows one to develop a distribution species model based on its presence in a series of particular points. The software generates a predictive model of species distribution based on the obtained data and indicating probable places of occurrence.

With further climate warming, regardless of the scenario, it will follow, the climatic range of *A. dorsalis* in Europe and neighboring countries will shift: it will significantly expand north, northeast, and east while narrowing in the southern regions.

The tendencies in the range shifts of *A. dorsalis* allow us to presume that the species will further shift its range, which will partly fail to coincide with the range of its food objects. Distortion of the biotic relationships in field agrocoenoses, where the species is currently one commonest entomophages, may lead to an increase in the

number of phytophages and distortion of the natural mechanisms of pest number regulation in territories not yet used in arable agriculture. This ground beetle is an important object for monitoring the condition of natural and agroecosystems sensitive to intensifying global climate change.

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Supplementary material 1

Map 1. Points of occurrence of *Anchomenus dorsalis*

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Data type: images

Explanation note: Map of *Anchomenus dorsalis* distribution in Europe.

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